PRELIMINARY STUDIES ON ANTHOCEROTAE

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1. Generic-Subgeneric Limits in Anthocerotaceae

Introduction: In the completion of the last volume of my The Hepaticae and Anthocerotae of North America for Columbia Univ. Press, the MS of which is now in the publisher's hands, a last task was to revise the Anthocerotae.

My initial treatment of that group was prepared in 1953-56 while I was at Duke University; it underwent substantial revision after study of plants from south Chile, collected in October, 1969; it underwent further refinement after study of the New Zealand taxa, first in 1961-62, again in 1976 and 1984. The following attempt at an evaluation of supra-specific concepts was initially prepared in 1976, after consideration of the Australasian taxa. Philosophical concepts for any such attempt derive from the following considerations: (1) No major progress in comprehension of the group will result until the innumerable poorly known taxa are assigned to supraspecific groups. (2) Subfamilial and subgeneric categories are currently unemployed in the Anthocerotales; their utilization will give us additional "depth" in any hierarchy to be set up. Use of the subgenus category, especially, seems long overdue; its use will also mediate between extreme taxonomic positions. A single example: the taxa placed by Hasegawa (1984) in Folioceros were regarded by Proskauer to be congeneric with Anthoceros s. lat. (Aspiromitus in the sense of this paper). I here accept an intermediate position and would recognize Folioceros as an autonomous subgenus. (3) Unless and until biochemical or other criteria so far undiscovered come to light, our classification must remain "conservative" since morphological and anatomical criteria -- the only criteria currently employed in constructing a classification -- are few, and the organisms exhibit considerable phenotypic malleability. Indeed, the exceptional architectural uniformity of the Anthocerotae is linked with equally exceptional levels of phenotypic (and probably genotypic) variation. Recent study of the spermatids of Anthocerotales thus far fails to reveal significant differences between those of Anthoceros s. lat. and Notothylas (Renzaglia & Carothers, 1986). Reluctantly, I must conclude that the Notothylaceae are best regarded as merely a subfamily of Anthocerotaceae.

The classification of the Anthocerotaceae remains a "dark chapter" in part because the approximately 200 binomials have yet to be fully digested. As with, e.g., Riccia, herbarium material is hardly suitable for critical study. Even the generic/subgeneric position of many taxa remains to be established and most will surely

prove to be synonyms of widely disseminiated taxa. The following attempt at an overall generic/subgeneric classification represents the best that I can derive at the moment; the following data serve as an effort at justifying this classification. Some of the rationale for the grouping accepted will be elaborated in the last volume of The Hepaticae and Anthocerotae of North America.

I have repeatedly evaluated extant concepts of genera and subgenera in the Anthocerotales. Indeed, aside from the single case of treating Phaeoceros as a subgenus of Anthoceros by E. Jones (1958), subgenera have not been adopted in the Anthocerotaceae. This is an error: understanding of the many poorly known taxa in the group can only be achieved if the species are organized into comprehensible units. Thus all three genera, Aspiromitus Steph., Megaceros Campb., and Dendroceros Nees are here divided into pairs of subgenera. This, at least, allows us to organize the taxa into more readily grasped units. I am convinced that the two new subgenera recognized (Megaceros subg. Nothoceros, Dendroceros subg. Apoceros) and Aspiromitus subg. Folioceros are natural groups; the level at which they are to recognized remains conjectural. Thus Haessel (1963) goes so far as to unite Dendroceros and Megaceros, while Proskauer refers taxa to Dendroceros that I would place into Megaceros. I would agree with Hasegawa (1983) that Megaceros is adequately defined and would further agree with him in limiting Dendroceros to taxa with multicellular (= precociously germinating) spores. I would agree with Proskauer that the form of the pseudoelaters is inadequate to separate species such as those assigned by Hasegawa (1984) to Folioceros as as autonomous genus, but would move in Hasegawa's direction to the point where I would recognized Folioceros as a distinct subgenus. It is thus evident that my taxonomic concepts fall somewhere between the overly conservative and the rather radical. Before further divisions are attempted, detailed studies, based on living plants, especially of antheridial structure, are badly needed. Since both lack of living material, and time, preclude my currently going into the matter in more detail, the following synopsis (taken with slight emendation from The Hepaticae and Anthocerotae of North America) is presented. In order not to clutter up that work with details on exotic taxa, and Latin diagnoses, these are briefly given here (under Footnotes).

Synopsis of Subfamilies, Genera and Subgenera:

I. Sporophyte erect, filiform, emergent, dehiscent by 2 valves; persistent basal meristem present. Pseudoelaters usually elongated, differing in size and form from spores, usually septate. . . . II.

II. Sporophyte with stomata distinct in the 4-5-stratose wall. Pseudoelaters devoid of spiral thickenings. Spores not green prior to germination. Gametophytic cells with solitary chloroplasts. Usually 2-many antheridia per chamber.

subfam. Anthocerotoideae. . .1.

1. Spores yellowish, not areolate on external face. Thalli solid. Antheridia with many-celled jacket, the cells not tiered.

Anthoceros L. [Phaeoceros Prosk.]

1. Spores fuscous to black, usually (at least imperfectly) areolate, at least on distal face. Thalli with conspicuous cavities. Antheridia with few, mostly elongated, tiered jacket cells.

Aspiromitus Steph., s. lat. . . 2.

2. Pseudoelaters usually highly irregular, wall ± thin, not regularly 4-celled.

subg. Aspiromitus

2. Pseudoelaters always slender, wall thickened, regularly 4-celled.

subg. Folioceros (Bharadw.) Schust.

II. Sporophyte with stomata lacking; wall 4-5- or 8-16-stratose. Spores green within capsule. Pseudoelaters with spiral thickenings. Antheridia 1(2) per chamber.

subfam. Dendrocerotoideae subfam. n. . 3.

3. Capsule abbreviated, with 4-5-layered wall. Thalli nonradiate, sparingly furcate; apical cell hemidiscoidal. Spore with endosporic development, pluricellular prior to release. Columella slight, 16-celled in cross section.

Dendroceros Nees. . . . . 4.

4. Costa (midrib) solid. Thallus wings simply perforate, infrequently with larger lacunae.

subg. Dendroceros
[Type: D. crispus (Sw.) Nees]

4. Costa lacunose or cavernose. Thallus wings with lacunae.

subg. Apoceros Schust., subg. n.
[Type: D. cavernosus Hasegawa]

3. Capsule filiform, elongated, with wall usually 8-16-layered. Apical cell (when known) wedge-shaped. Spores 1-celled at time of release. Columella (when known) massive, to 40-celled in cross section.

Megaceros Campb. . . . . 5.

5. Thalli radiate, closely dichotomously branched, with very abbreviated segments.

subg. Megaceros

5. Thalli nonradiate, remotely furcate, with lingulate to linear segments.

subg. Nothoceros Schust., subg. n.

I. Sporophyte horizontal or semihorizontal, ± fusiform, not or tardily dehiscent, covered until maturity by the perichaetium, lacking a persistent basal meristem. Pseudoelaters reduced, subspherical, similar to spores in form and size.

subfam. Notothyladoideae
Notothylas Sulliv.

Annotations: Several relevant comments as to this arrangement seem appropriate. But first I must note, as Proskauer repeatedly emphasized, that most described taxa are so poorly known, usually only from herbarium material, that distinctions used above may prove to be nonapplicable in individual cases. The following comments (and brief diagnoses and synonymy) are needed.

(1) One cannot ignore the fact that Aspiromitus is legally published and, as Proskauer himself noted, was based by Stephani very largely on the black-spored taxa. In the final volume of The Hepaticae and Anthocerotae of North America, an appropriate discussion of the relevant literature is found. As circumscribed by Stephani, the genus was far less heterogeneous than, e.g., virtually every genus proposed by Dumortier! The lectotype of Aspiromitus agrees with Aspiromitus as here accepted; it was valid in 1916 and widely accepted in succeeding years.

(2) The family appears to be divisible into 3 genus-complexes and criteria used in the above synopsis are generally applicable. I am aware that at least one species of Aspiromitus exists that lacks stomata; this appears to be a parallel, a secondary loss which does not necessarily invalidate the basic generalization.

(3) The Dendrocerotoideae[1] seem distinct in at least 4 non-related criteria, derived from capsule wall, spores, pseudoelaters and antheridial number.

(4) Folioceros Bharadw., in essence, was based on a single criterion: the thick-walled, 4-celled pseudoelaters. Although certain authors (e.g., Hasegawa, 1984) accept this taxon at the generic level, I think subgeneric status more accurately reflects the level of discontinuity. Aside from the solitary pseudoelater criterion, Hasegawa (1984) utilizes two other distinctions:

Aspiromitus (Anthoceros sensu Proskauer)	Folioceros
Spores "always with conspicuous triradiate marks, without conical or mammiform outgrowths."	Spores "often with indistinct triradiate marks, when with conspicuous triradiate marks coni-

	cal to mammiform outgrowths present."
Epidermal cells of capsules with fairly large lumina	Epidermal cells of capsules with narrow, linear lumina.

Regarding these two distinctions, the following points are relevant: (a) in the A. macounii-adscendens complex the spore exine bears superficial tubercles of all faces, much as in "Folioceros" fuciformis (Mont.) Bharadw. (cf. Hasegawa, 1984, fig. 10:a-b and Schuster, 1966, fig. 10:3); in A. adscendens (A. ravenelii) the triradiate ridges are considerably reduced vis a vis such typical Aspiromitus species as A. punctatus s. lat. The spore criteria in these taxa are clearly intermediate between the two extremes recognized by Hasegawa. (b) The degree to which the epidermal capsule-wall cells are incrassate is subject to wide variation. Thus Proskauer (1958, p. 1306, fig. 509:c, g) draws the capsule-wall cells of A. caucasicus and A. mandoni (both with Aspiromitus-type elaters) with the lumina virtually as narrowed, and the longitudinal walls as thickened, as in, e.g., "Folioceros" fuciformis (cf. Hasegawa, 1984, fig. 10:j).

At best these two distinctions represent quantitative distinctions. I would agree with Proskauer in retaining the species subsequently segregated into Folioceros within the larger genus Aspiromitus (Anthoceros sensu Proskauer), but grant that subgeneric status for the Folioceros species is appropriate. [2]

(5) Megaceros subg. Nothoceros Schust., subg. n.[3] The two taxa I refer here were placed by Proskauer (1953) into Dendroceros, but he admitted that with M. endiviifolius one runs into "the difficult problem of the definition of. . . Megaceros and Dendroceros." Haessel (1963, p. 32) also referred Megaceros fuegiensis Steph. to Dendroceros, widening the concept of Dendroceros even further. However, Dendroceros s. str. differs from Megaceros not only in the criteria used in the above synopsis, but also, in general, as follows: (a) the costal region is reduced and the "wings" widely expanded, normally perforate; (b) epidermal cells of the capsule wall are little elongated, typically 1.5-3.5:1, with conspicuous convex-sided thickenings at the angles (cf., i.a., Hasegawa, 1980, fig. 1:g-h; 1981, fig. 1:9) ranging to moderately elongated and 3.5-5:1, with very thick and confluent longitudinal walls (cf. Hasegawa, 1980, figs. 3:i-j and 5:f). In nearly all Megaceros species the cells are linear (Haessel, 1963, pp. 30, 32) or regularly short-oblong (Hasegawa, 1983), never developing thickenings at the angles. I would thus agree with Hasegawa (1980) in retaining Megaceros as a distinct genus and would solve the problem of the two nonradiate taxa, which seem superficially intermediate between Megaceros and Dendroceros, by placing them into an autonomous subgenus within Megaceros. This is admittedly a tentative classification. Chloroplast number may yet necessitate alterations in this system.

(6) Dendroceros Nees includes two widely different species-com-

plexes: (a) one complex, typified by the generic type D. crispus (Sw.) Nees, has a solid costal region and the thallus wings bear simple perforations between cells (cf. fig. 2 in Proskauer, 1960); belonging here are, i.a., D. japonicus Steph., D. tuberculatis Hatt., D. subplanus Steph., D. foliicola Hasegawa, D. acutilobus Steph., D. validus Steph., and D. borbonicus Steph. (b) A complex typified by D. cavernosus Hasegawa, D. difficilis Steph., and D. pedunculatus Steph. in which the costa varies from lacunose to cavernose. For this complex I propose the subgeneric epithet, Apoceros Schust., subg. n.[4]

Among recently studied species, D. javanicus (Nees) Nees appears to form a transition: it has a solid, biconvex costa, but has lacunae of the thallus wings (cf. Hasegawa, 1980, fig. 8). So apparently does D. granulatus Mitt. (Hasegawa, 1982).

One problem remains that I have been unable to solve for want of adequate material: in the generic type the pseudoelaters are 4-celled, as in Aspiromitus subg. Folioceros (cf. Proskauer, 1960, fig. 4), while Hasegawa (1980), when he illustrates entire pseudoelaters, shows them to be uniformly 1-celled (cf. figs. 5:g, 8:k).

The primary basis for dividing Dendroceros into two groups, in my opinion, must be costal anatomy. Stephani (1909) already recognized this fact. Unlike the situation with the Anthoceros-Aspiromitus complex, however (where we also see the solid vs. lacunose dichotomy in thallus structure), the difference in thallus anatomy in Dendroceros is not adequately linked with other criteria -- as the example of the D. javanicus-granulatus complex appears to show.

Taxa with a cavernose costa appear to form a well-defined complex also on the basis of capsule anatomy. The species illustrated by Hasegawa (D. cavernosus, D. pedunculatus, D. difficilis) all have elongated (2.5-5:1) epidermal cells with longitudinal walls strikingly and almost uniformly thick-walled (cf. figs. 9:g, 10:f, 11:f in Hasegawa, 1980). By contrast, taxa with a solid costa show wide deviations in form of epidermal capsule-wall cells. Thus the anomalous D. javanicus complex has epidermal cells identical to those seen in Apoceros (cf. fig. 8:g in Hasegawa, 1980); so does the generitype, D. crispus (cf. Proskauer, 1960, fig. 3).

Most taxa with a solid costa, however, and with simple perforations of the wings show abbreviated (1-2.5:1) epidermal cells, strikingly thickened at the angles, but with lateral pitlike, thin connections between adjoining cells (cf. fig. 1:g-h, in Hasegawa, 1980), although others have such strikingly thickened cells that lumina become linear (e.g., D. acutilobus Steph.)

As a consequence, capsule-wall anatomy does not support any subgeneric link, at least as understood at present.

(7) Notothyladoideae (K. Müll.) Schust., stat. n. [Basionym:

Notothylaceae K. Müller, Rabenh. Krypt.-Fl. 6, Erganz. Bd.:200, 1940.] In my opinion it is better to classify the Anthocerotaceae into 3 rather than 2 subfamilies. The 3 groups represent steps in reduction. Thus the Anthocerotoideae are generalized in: (a) retaining stomata; (b) the usually short involucrum or perichaetium; (c) the relatively unspecialized pseudoelaters. The Dendrocerotoideae have undergone some reductive evolution; (a) they have lost stomata of the 2n generation; (b) they tend to develop, in Dendroceros, more abbreviated sporophytes, with the perichaetia becoming tubular and elongated. This linked with evolution of one major specialized trait: the spiral elaters. In the tendency toward reduction in length of sporophytes and evolution of longer perichaetia, linked with loss of sporophytic stomata, Dendroceros foreshadows the more massive reduction we see in the Notothyladoideae; here perichaetia are expanded and sporophytes even more reduced. Associated with the general reduction of the sporophyte, the columella has undergone varying degrees of reduction. I do not wish to suggest that the Dendrocerotoideae gave rise to the Notothyladoideae. Rather, both subfamilies show parallel reductive tendencies -- that of the Notothyladoideae clearly more marked. Tendencies toward sporophyte reduction already crop up in the Anthocerotoideae, e.g., in Aspiromitus macounii. As a consequence we should not assign too much significance to sporophyte size, or simplification, in the Notothyladoideae. No new feature has evolved in this last group: Notothylas, indeed, differs from Anthocerotoideae principally in the horizontal capsules. Admittedly reduction in pseudoelaters in Notothylas has reached an end point -- yet comparable reduction already exists in taxa such as Aspiromitus macounii (Howe) Schust., comb. n. [Anthoceros macounii Howe, Bull. Torrey Bot. Club 25:19, 1898]; cf., e.g., Schuster (1953, fig. 16:2-4). There seems to be a general tendency in terrestrial Anthocerotae for capsule reduction linked with pseudoelater reduction, as seen not only in A. macounii, but also in Aspiromitus adscendens (L. & L.) Schust., comb. n. [Anthoceros adscendens Lehm. & Lindenb., in Lehmann, Nov. et Minus Cogn. Stirp. Pug. Quart., p. 24, 1832], as is shown in Frye & Clark (1937-47, p. 941, figs. 6-8).

2. Aspiromitus appalachianus Schust., sp. n.[5]

Similar to the A. punctatus crispulus phenotype in the crispate and freely lamellate thalli; distinct from A. punctatus and virtually all other taxa of Aspiromitus in the sharp distinction between a spinose-areolate external spore face and plane, only obsoletely sculptured inner spore faces. Type. North Carolina: Toxaway R., Transylvania Co. (RMS 45231). Known again only from above Jocassee, Estatoe Cr., South Carolina (RMS).

This species is described and illustrated in detail in the final volume of The Hepaticae and Anthocerotae of North America; here only the Latin diagnosis is given, since material of the species (labelled Anthoceros appalachianus) by now has been widely distributed during the last three decades.

I know of no member of Aspiromitus in which the strongly spinose-foveolate external spore face is contrasted more strongly to the inner (proximal) spore faces.

Acknowledgement: I thank Dr. Hannah Croasdale for generously preparing the Latin diagnoses.

Footnotes

[1] Subfam. Dendrocerotoideae Schust., subfam. n. Subfamilia a Antherocotoidis differens quod (a) sporophyta sine stomatibus; (b) elateres spirales; (c) omnis locellus antheridialis 1 vel 1(2) antheridia continet. Type: Dendroceros Nees.

[2] Aspiromitus subg. Folioceros (Bharadw.) Schust., status nov. Basionym: Folioceros Bharadw., Geophytology 1(1):9, 1971. Type: Aspiromitus assamicus (Bharadw.) Schust., comb. n. [Basionym: Folioceros assamicus Bharadw., ibid. 1(1):9, 1971].

[3] Megaceros subg. Nothoceros Schust., subg. n. Subgenus a subg. Megacerote differens quod thalli raro ad sparse furcati, segmentis linearibus ad ligulata; a Dendrocerote differens quod sporae tempore liberationis unicellulares. Type: Megaceros endiviaefolius Steph. (M. endiviifolius) of South America; M. giganteus (L. & L.) Steph. of New Zealand also belongs here.

[4] Apoceros Schust., subg. n. Subgenus a subg. Dendrocerote differens: (a) costa cavernosa aut lacunosa; (b) alae thalli lacunosae aut perforatae, lacunis magnitudine variantibus. Type: D. cavernosus Hasegawa (1980, p. 306, fig. 11).

[5] Aspiromitus appalachianus Schust., sp. n. Species A. punctato crispulo phenotypo similis quod thalli crispati et libere lamellati; distincta ab A. punctato et fere omnibus aliis taxis Asperomiti quod superfacies externa sporae spinoso-areolata bene distincta e superficiebus sporarum internis planis et modo obsolete sculptis.

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